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OBSERVATIONS ON THE BEHAVIOR OF TUBICOLOUS ANNELIDS. III.

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In two earlier papers dealing with the general subject of the behavior of tube-dwelling annelids the writer endeavored to give in some detail an account of experiments and observations made upon several species of these worms available at Woods Hole, and incidentally made reference to a few observations upon one of the Naples species, *Protula protula*. During a recent occupancy of the Smithsonian table at the Naples laboratory occasion was taken to extend these observations to several other species, and to make as critical a comparison as might be practicable of the behavior of the latter with that of the Woods Hole species. It will be noted that in the present account less attention has been given to details of time reaction, various stimuli, etc., than before, and that behavior in relation to light has been emphasized. This was deemed the more important since it was upon these species that some of the earlier work concerned with animal heliotropism was done. As may be recalled, my work already mentioned ('06, '09), did not tend to confirm these views; and it was with a view to test them by a repetition of the experiments that I undertook to reëxamine the subject. In the following account will be found the results and conclusions which my observations have seemed to warrant.

The following are the species which have been used: *Protula protula*, *Hydroides pectinata* (*Serpula uncinata*), *Pomatoceras triqueter*, and *Spirographis spallanzanii*. The experiments were carried on from January 1 to April 15, a period of three and one half months. Particular pains were taken to vary the experi-

ments in every practicable way, and under a range of conditions which would eliminate as fully as might be errors of inference based on limited experiments or faulty environmental conditions. Details on these points will be given in later sections of the paper.

Protula protula.

This annelid is a very familiar element of the fauna of the Bay of Naples. Its large size, often 175 mm. in length by 5–8 mm. in diameter, its fantastically coiled tube, and the brilliant orange-red gills which are splendidly displayed during expansion conspire to make it a conspicuous object. The sensitiveness of the creature to differences of light intensity, such as that involved in the intervention of shadows, was one of the first aspects of behavior to engage my interest many years ago, some brief notice of which was made in my early paper ('06, pp. 311, 314). These observations I have verified again and again during the present series of experiments. Careful comparisons of many specimens in their reactions reveal the fact of marked individuality as expressed in the variability of behavior shown from day to day. It is not necessary to go into details concerning this point. What has been pointed out in the case of *Hydroides dianthus* ('09) is confirmed in the case of *Protula*. Certain specimens were especially sensitive and extremely active in response, while others would show the very opposite; and it was not unusual to find specimens which seemed totally indifferent to shadow stimuli. Again, specimens might prove quite sensitive at a given time and very indifferent at another. But let it be noted that some specimens seemed normally to be highly sensitive, while others seemed normally quite the opposite. Again, the retraction aspects of behavior, that is, the time a given specimen remained in the tube after a given contraction, was remarkably variable. In some cases the emergence was relatively prompt, while in others it was extremely slow. In this matter *Protula* differs materially from *Hydroides*, whose retraction periods are usually and normally very brief. *Protula* often remained retracted for indefinite periods, often for one or two hours at a time, in marked contrast to *Hydroides*.

Tubular Aspects.—The behavior of *Protula* as expressed in the

form or aspects of the tubes is noteworthy. In my early paper was shown a figure which made this very graphic. No less than in the case of *Hydroides* the tubes of *Protula* show the record of erratic behavior in very striking manner. (Cf. '09, pp. 180–183.) During early life these tubes usually adhere very strongly and closely to the base of support; but in maturity they often incline more or less toward the vertical, though in a rather sinuous or spiral direction, or may even coil about each other and assume

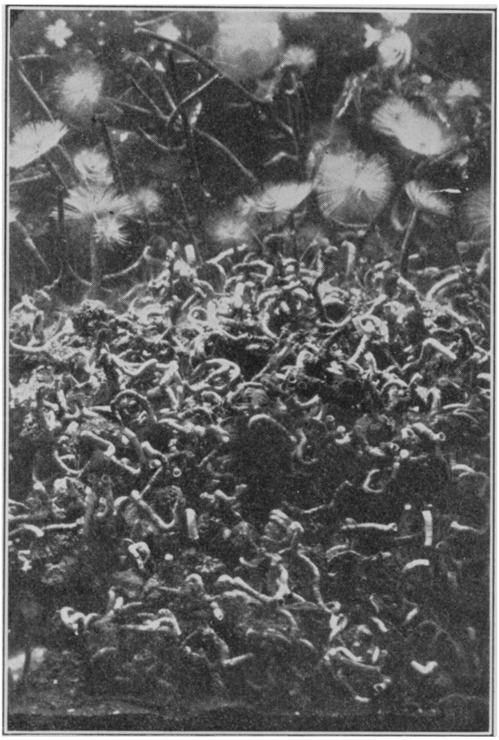


FIG. 1 shows a large colony of *Protula*, with *Spirographis* in the upper part. The promiscuous curving of the tubes is very marked.

a downward aspect. This may be seen most strikingly in the large colonies of these creatures always present in the show aquaria of the laboratory, where may also be seen to best effect the marked variability as to tubular behavior. Something of this is graphically shown in Figs. 1 and 3, copied from photo-

graphs taken by Dr. Sobotta, by whose kind permission I am able to present them here. As will be seen, the aspects of the tubes and of the openings through which the creatures protruded their heads are so extremely diversified as to seem to be absolutely chaotic. If one may distinguish any tendency toward a given aspect of position, still the departures are so numerous as to render it almost certain that no single factor could have been determinative. As in the case of *Hydroides* ('09, p. 180, etc.), *Protula* has left in its tubes a convincing record of the erratic individuality of its behavior the significance of which is extremely important.

Autotomy.—In this connection may be considered a feature of behavior more or less unique, though not peculiar to *Protula*, since it has been noted in several cases of *Spirographis*; namely, that of autotomy, or the self-excision of certain organs of the body. This was first observed in the case of *Protula*. A specimen of this worm was among the first to come under my observation, having come to my table almost the first day in the laboratory. It had been placed in a small aquarium jar on the table for convenience of study. After finishing a given series of tests the specimen was usually returned to the large aquarium. On January 7 the specimen had been under observation and was left in the table jar which had a capacity of about four or five liters, while I went out to lunch. This could hardly have been more than an hour or so, but on return I observed what seemed strange—the detached portion of about half of the gill mass lying at the base of the tube. An examination of the gill failed to reveal any signs of disease or other abnormality. My first impression was that possibly the water had become "*bad*," yet other living things, such as copepods, showed no signs of discomfort. However the water was renewed several times during the afternoon and the specimen finally left on the table over night, as had been done several times before. The following morning upon examining the jar I found the other portion of the gill in the same detached condition, lying at the base of the tube, but the specimen was deeply retracted within the tube. After some time it came to the orifice and showed clearly that it was entirely devoid of gill elements. It was now transferred to the

large aquarium and left to see whether regeneration would occur and if so at what rate. For a few days it frequently came to the orifice and extended the mantle edge over the margin of the tube and remained in that condition for some time. Later it again withdrew deeply into the tube and did not show itself for several days, indeed for some three weeks or more. Finally, on February 13 it was once more seen to protrude its head, but there was not the least sign of any regeneration. Its appearance now became more frequent and occasion was taken to test it by shadows, and to my surprise it was found to react as promptly as at the very first. These tests were made many times on subsequent days with the almost uniformly prompt and positive reaction, but with the variations observed at first, *i. e.*, sometimes less sharp, and then more so, and occasionally not at all.

Several interesting questions arise in this connection. First, as to the regenerative capacity of *Protula*. For nearly two months not a sign of regeneration was distinguishable. I had previously recorded ('06) the promptness with which *Hydroides* regenerated its gills, and similar records had also been made by Zeleny. Finally on March 14 I found undoubted evidence of regeneration, and this went forward apparently rather rapidly; for by April 10 the new gills had become quite conspicuous—nearly a fifth as large as the originals. It may be noted here that later I had also a similar autotomy by another specimen of *Protula* and by two specimens of *Spirographis*. In these cases there could not be doubt as to any condition of water inducing the autotomy, for the specimens continued to thrive, as did many others in the same tank. Regeneration was very prompt and rapid in these cases.

A second point is in relation to such correlation of function as would enable the creature during this long period of gill deprivation to maintain the normal respiratory activity. If respitation were restricted to the gills alone of course it must have perished. This experiment shows clearly that this function may be taken up by other organs of the body without serious inconvenience. But the gills are also concerned in the process of nutrition, acting as a medium for capture of prey. How might this function have beeen supplemented? It has

been said that during this time the specimens remained rather continuously within the tubes. Did they depend wholly upon a reserve food supply?

It may not be possible to answer these queries fully, but of the correlation of the skin in the function of respiration there can be no serious doubt. In my earlier experiments on *Hydroides* ('06) it was found that when the gills were excised to test their relations to sensory reactions the creature did not seem to suffer any serious inconvenience as to respiration. So in the case of *Protula*, there was no evidence to the effect that respiration was not normal during the long period of gilless life. Bounhiol (1900) has reached similar conclusions from experiments on *Spirographis*. He finds that respiration takes place through both skin and gills, and that they supplement each other by compensatory interaction. He finds also that it is apparently easier for the gills to assume extra work than for the skin, and that in excretion of CO_2 the skin normally excretes about three fourths of the entire amount.

In the third place, there is the interesting query as to the sensory function. I have shown that for *Hydroides* light perception is almost exclusively a function of the gills. In *Protula* this is not so certain. Its behavior in this respect is less easily controlled, owing to the sulking disposition of the worm. But it is quite certain that autotomy did not result in entire inhibition of reaction to shadows and it may not be improbable that something of sensory compensation may obtain in this, as in the respiratory activity; or possibly this sensory function may be shared in part with some other head-organ; possibly the mantle margin, which in normal life is often extended over the orifice of the tube, hence in a position admirably adapted to such a function.

Concerning the entire matter of the significance of autotomy little can be said. Such phenomena, similar in many respects, are well known among other animal groups, though not common in any case, unless we may include phenomena of fission which is a very familiar feature in many annelids; but this seems to be a wholly different problem. That it is spontaneous, hence not attributable to the operation of gravity, contact, etc., seems very evident.

Pomatoceras triqueter.

This, with an undetermined species of *Serpula*, are tubicolous annelids which much resemble in general aspect of size, structure and behavior, *Hydroides dianthus*. Indeed in almost every particular they might have been substituted for the latter species without marked changes of results. In general habitat the two species are much alike and often found growing on the same substratum. *Pomatoceras* is rather larger, and its tubes are characterized by rather sharp triangularity with the dorsal angle forming a sharp crest along the entire tube. No attempt will be made to go into details as to matters of behavior, since as already suggested, they show the same reaction phenomena as those given in the accounts of *Hydroides dianthus*, and the growth aspects are quite as erratic. For the most part the tubes adhere closely to the substratum, and in some cases they adjust themselves with such nicety to grooves or similar depressions that one might guess they were under the control of some such stimulus as thigmotaxis or stereotropism. But when one comes to examine any considerable number of specimens he soon finds that in by far the larger number there is absolutely no such adjustment. The same is the case with *Hydroides*. Now and then a specimen may be found on a shell of *Pecten* in which there is a very fine illustration of such *appearance*, the creature having kept very closely and exactly in the radial grooves of the shell. But on the same shell may now and then be found another specimen which has grown directly across these grooves; and of course by far the larger number have absolutely no semblance of such response. The conclusion is therefore forced upon one that the operation of any such factor must be, if not wholly nil, yet of only incidental significance in behavior.

Again, in habitat one finds in the Mediterranean species the same wide range as in those of Woods Hole. I have dwelt upon this point with some emphasis in a former paper ('09, pp. 182–3), and need only refer to the matter in this connection by way of further emphasizing a point which I regard of considerable significance. The growth of these organisms indiscriminately on a large variety of substrata, rocks, shells—the latter both dead and living—nets, crabs, lobsters, etc., is itself of no small

import as to the negative influence of such factors as light, gravity, etc., in relation to growth. This is further borne out by attention to the aspects of the several tubes which may comprise a given colony. In several such an actual count of the growth direction was made. On a stone which contained 37 living specimens I found that 12 had a general upward direction; 15 had just as definite a downward course; and 10 had a horizontal direction. Another colony growing on the inside of an iron cup about 6×10 cm., made up of eleven specimens, showed the following disposition as to direction: 4 upward, 5 directly down, and 2 horizontal. On the outside of the same cup were eighteen specimens disposed as follows: 8 upward, 7 downward, and 3 horizontal. These plainly go to confirm the conclusions already drawn, that in the matter of orientation one is utterly unable to discover the operation of any one or several factors which are in any sense determining.

Hydroides pectinata.

This species and the one described in the following section, *Spirogaphis spallanzanii*, were the ones used by Loeb in his well-known experiments at Naples many years since, the results of which, including also several species of hydroids, served as a basis for his far-reaching theory of animal heliotropism, especially as it relates to sessile animals. Naturally, therefore, more of details will be expected in the following accounts than in the preceding, and I shall endeavor to make explicit and definite records both of methods and results.

Hydroides pectinata (*Serpula uncinata*) is one of the most common and abundant of the Naples annelids. Unlike *Spirographis*, it grows usually in immense colonies, aggregating hundreds or perhaps thousands of individuals. Fig. 2 will give a general idea as to their appearance in small colonies. The tubes of a given colony form a mass of more or less parallel aspect, the individuals apparently growing at approximately the same rate and in the same general direction. When one casually examines such a colony it would seem to afford a typical illustration of orientation due to some single constraining stimulus. But here again, as in the case cited above as to stereotropism, extended

observation brings to light too many exceptions to any such rule, and compels further inquiry. Like other species of *Hydroides* this one secretes a calcareous tube, the shape of which depends upon the mode of growth of the individual constructing it. Hence in aspect, size, etc., these become permanent records of everyday behavior, whether this be mechanical, ecological, or physiological in its nature. Several colonies were put under

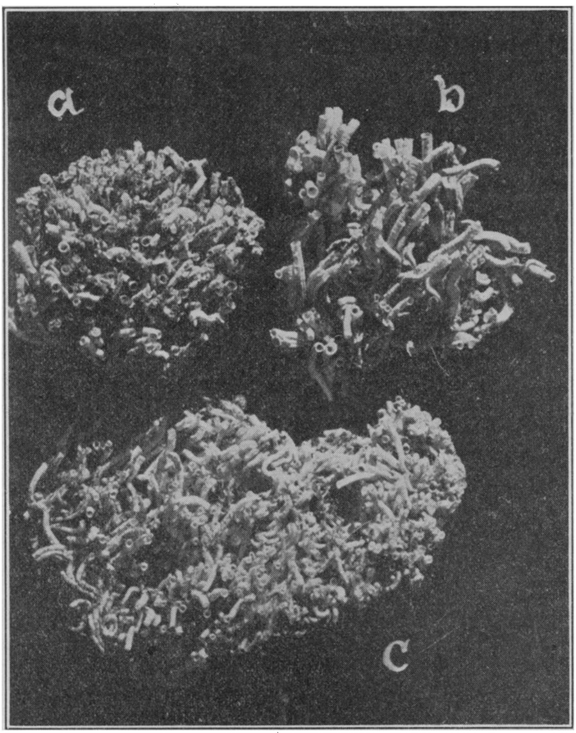


FIG. 2, *a*, *b*, *c*, shows three colonies of *Hydroides pectinata* which have been under light test for more than a month. As will be seen the curvings of the tubes are much as in Fig. 1.

observation early in January and were tested during a period of more than three months; to be more exact, from January 3 to April 12. They were tested as to the possible influence of both light and gravity. Loeb claims that in this species the reaction is quite prompt. "I noticed that in the course of the next day

the Serpulidæ, which like *Spirographis* presented only their gills to the light, bent them strongly upward" ('90, "Gen. Phys.," Part I., p. 102), and he continues, "within six weeks the entire block was covered with tubes which curved upward; not a single individual had continued to grow in the original direction," and presents a figure in illustration. There is apparent discrepancy between the latter and the statement "*not a single individual*, etc.," for in the figure about as many appear to "continue to grow in the original direction" as have "curved upward." My own experiments show a reasonable conformity to Loeb's *figure*, but the ratio of tubes indicating reaction is very much smaller. Figs. 2, *a*, *b*, *c*, are photograph reproductions, and may therefore be taken at their face value, and they certainly fail to show any such response as claimed above. For example, it was found by actual count of a colony comprising hundreds of tubes which had been under test for more than a month that only about twenty tubes had definite curves toward the light, a similar number had shown lateral curvatures, and a smaller number had curved downward; but the larger number "had continued to grow in the original direction." A smaller colony which had been under test for twenty-five days under particularly favorable light conditions showed a slightly larger response toward the light; but here also the number was relatively small. Another colony was placed in an aquarium which was covered on three sides and above with a black hood. After a test of nearly two months (January 23 to March 18), it was found by a careful estimate from counting that at most only about 20 per cent. showed any possible light reaction; while by far the greater number either continued to grow in the original direction or showed curvature laterally or downward. The colony was submitted to two others working at the laboratory, Dr. Butler, of University College, Dublin, and Dr. S. R. Williams, of Miami University, Ohio, both of whom made the per cent. of light reaction much lower than my own.

A very interesting and, I believe, significant feature of growth in this species came to light during the observations, namely, its very erratic, or discontinuous character. Some individuals showed a very prompt and rapid growth at first and later its

cessation. In this process of rapid growth some show a bending while others do not. Again, some bend toward the light, others away from it, and still others continue in the original direction. The point of importance here is not the bending or curving, but simply the *tube-extension*. This extension is not, as I interpret it, an expression of *growth* at all, so far as the body mass of the animal is concerned. Seldom are aquarium conditions especially conducive to *physiological growth*. What then does such tube-extension mean? Isolated worms lying side by side, of essentially similar age, state of vigor, under identical conditions, show the most remarkable differences in relation to this matter of so-called growth. One may in the course of a week extend its tube 3–5 mm.; another shows not the slightest extension of its tube. One may extend its tube in the line of the body axis, *i. e.*, straight, the other show a sharp curvature from the first. There has been equal access to food, air, light. Why has not growth been the same in direction and amount? As a matter of fact it may be doubted whether there has been any appreciable growth. Indeed may not these erratic phenomena express just the opposite, namely, *lack of growth conditions*, or some other factors conducive to comfort? And if so then this erratic tube-extension is but an expression of such discomfort,—an expression of the efforts of the creature to seek better conditions, to reach out, as it were, in search of food, air, etc. Indeed, if my interpretation be correct, these curvings are but the natural expressions of efforts at food-getting or respiration—adjustments to those particular ends involved in survival or selection. In the light of this interpretation the real factors involved in these aspects of behavior are *intrinsic* and not *extrinsic*. The latter are conditional and passive; the former are individual, active, causative.

Spirographis spallanznii.

This species differs most markedly from those already considered in that it possesses a very flexible tube, hence is capable of considerable range of movement within a region measured by the radius of its own length. It is a large species at maturity, averaging perhaps about 25 cm. in length, by about 1 cm. in diameter. In my experiments care was taken to have specimens

of various sizes, and those actually used ranged from about 5 to 30 cm. in length. No less care was exercised as to conditions under which experiments were conducted. Three of the large aquaria supplied with running water were at my disposal during

FIG. 3 is a portion of one of the large show-aquaria containing *Protula* and *Spirographis*. The varied aspect of the latter is quite marked, as will be seen by comparing specimens in various positions.

the period, and in addition two special experimental aquaria of smaller size, about 25 × 35 × 45 cm., also supplied with running

water, were employed for such experiments as called for a critical control of light, etc. Of the large aquaria two were in a room with north exposure, and hence with diffuse light, but always adequate for ordinary observation and experiment; while the other was in a room with direct south exposure, hence with sunlight of almost any degree of intensity, modified by shades or screens. The two smaller aquaria were in a special room, the light of which was under easy control, and the aquaria themselves easily adjusted to any desired condition, as to amount and direction of light, etc. A still further point is worthy of notice. At all times I had free access to the large exhibition aquaria, where large numbers of these specimens were living under conditions as nearly natural as the long experience and painstaking skill of those in charge have been able to devise. I shall have occasion to refer to this in another connection.

During the progress of the experiments some fifty specimens were available, and the general health and vigor may be inferred from the fact that in the three and one half months not a single specimen died or even showed signs of deterioration, except as a slight fading of the brilliance of coloration may have been indicative of such. Care was taken to supply food from time to time, almost daily, such as came in from plankton hauls which were supplied to the rooms quite regularly, and this may have contributed to the excellent conditions of health already alluded to.

Spirographis seems to take rather naturally to the aquarium environment and soon becomes quite at home so far as one may judge from appearance. Specimens require from two to several days firmly to attach themselves to the bottom or sides of the aquarium. This is accomplished by an adhesive secretion of the worm which is discharged through a small pore at the lower end of the tube. The time required for attachment may be varied by having the bottom of the aquarium covered with a layer of sand or by placing fragments of rock in contact with the base of the tubes. While in most cases the specimens attach themselves wherever they happen to be placed, which is fortunate in such experiments as those under consideration, still it not infrequently happens that a specimen will go through various translatory movements before finally settling down. It may be noted that

these locomotor movements take place usually during the night. This I have demonstrated by carefully marking locations and noting subsequent changes. At no time have I found evidence of these movements during the day.

In general my experiments proceeded along the lines employed by Loeb ('90, *Arch. f. ges. Physiol.*, Bd. 47, p. 391), whose objective aim was to establish the essential identity of heliotropism in animals and plants, and his experiments were directed to that end. Incidentally it may be observed that he does not hesitate to claim "I think I have shown that the heliotropism of sessile animals is essentially identical with the heliotropism of sessile plants." And still later he asserts even more strongly, "It was possible to show that heliotropism of animals agree in every point with that of plants" ("Comp. Phys. of Brain," 1900, p. 181). It may be doubted whether, in the light of present knowledge, this would be seriously maintained. I shall not discuss the matter here further than to say that my own experiments were undertaken with a very different aim, namely, that of ascertaining the questions of fact,—*Are these organisms heliotropic?* and further, *Do they exemplify*, or *conform* to the *mechanical concept* of *behavior?*

In the following account I shall present the matter under some three distinct series. First, those experiments made in the aquaria located in a north room; second, those conducted in the smaller experimental aquaria; and third, those conducted in the large aquarium located in a room with exposure to direct sunlight.

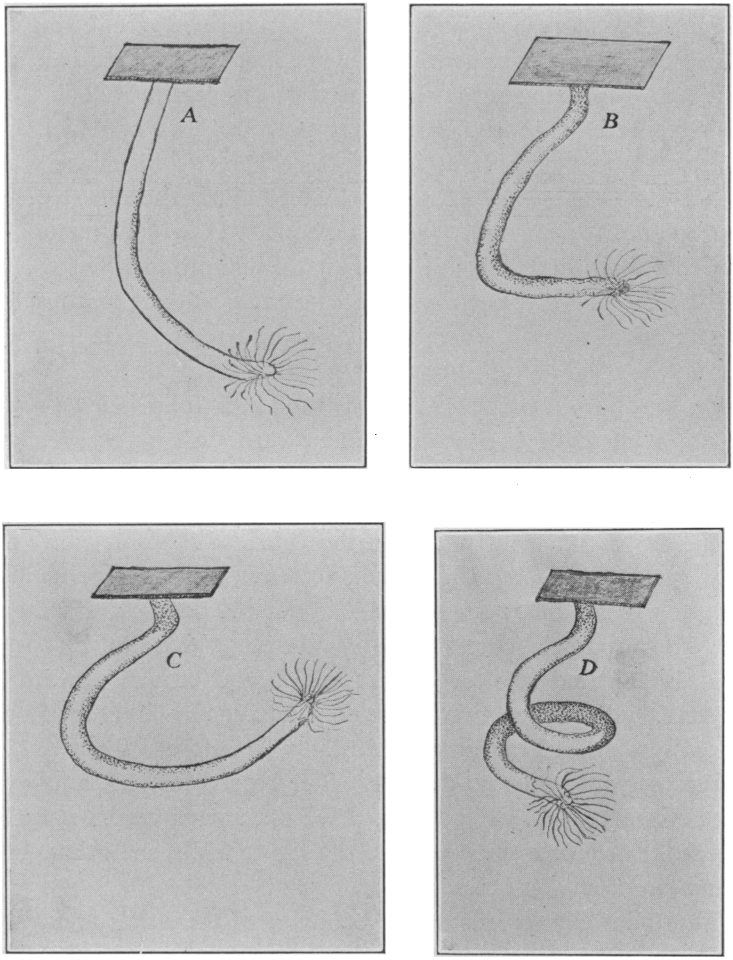
The first series began on January 6 with some six specimens. To these additions were made from day to day, till on the 13th I had twenty, which had been variously distributed in the two large aquaria, some with the heads directed away from the windows, others directed at right angles, and still others facing the windows. The aquaria were of about the same size, probably 1.5 meters in length, by about 40 cm. in depth and width; the one with its end toward the window, the other with its side toward the light. It was some time after specimens had become attached before any sign of orientation was discernible. In the aquarium (No. 1) with the end directed toward the light there were twelve specimens, in the other eight. The twelve had

been distributed so that three should face toward each of the sides of the tank; *i. e.*, three with heads directed toward light, three away from light, and six at right angles, three facing each side. On January 26 all specimens were attached except one, which for some reason, perhaps injury, remained free during the entire course of the experiment, hence may be disregarded. At this date the following is the record of orientation. The three facing the light continued in that position, one of which had assumed a nearly erect attitude; the other two had barely elevated the head to a degree sufficient to allow the gills to clear the bottom of the tank when expanded. Four specimens now face the wall, and all with barely sufficient up-bending to free the gills from the bottom. The laterally directed specimens continued as at first, except that one had made a distinct up-curve, the head elevated to an angle of about 35 degrees.

On February 6 the record of this tank is as follows: Of specimens facing light two are curved upward, one nearly vertical, perhaps 70°, the other about 45°, while the third remains as before, and this in spite of the fact that direct light is intercepted by a tufaceous mass bearing tubes of *Protula*, etc. The four specimens facing the wall have made considerable change. One had rotated through an arc of about 100 degrees, now facing the side, and with head elevated about 35 degrees. Another has also rotated to nearly right angles and curved upward 50 degrees. The other two continue unchanged. The specimens laterally disposed continue essentially as before, except an up-curve of from 30 to 40 degrees. The record for this aquarium on February 25 is as follows: Five specimens are now facing the wall, three continue to face the light, while the others continue essentially as before.

The following records of the behavior of the other aquarium, which may be called number two, are interesting. In this were placed eight specimens, two of which were suspended head downward, and in this position they attach themselves and continued for many weeks. The others were located with heads predominantly toward the wall, *i. e.*, away from source of light, only one facing light. In this tank but little sign of light reaction was distinguishable. The specimen originally facing the light

later curved to the wall and remained in that position during the entire time, while one of the specimens placed facing the wall later curved toward the light side.



FIGS. *A*, *B*, *C*, *D* illustrate certain aspects of a specimen which was suspended head downward. At *A* is shown the first indication of change of position; a further change is shown at *B*; this curvature has reached its limit in that form at *C*, and continued thus for several days, oscillating somewhat from side to side, but with no evidence of reaction to light. At *D* the sickle shape is converted into the loose spiral, which likewise continued for some days essentially as shown in diagram; as in the others, there was shifting and change but with no relation to light.

The most interest attaching to this experiment is the behavior of the specimens suspended. For several days both remained hanging downward. Finally one began to curve, and directly by a graduated process assumed the aspects shown in the diagram figures *A*, *B*, *C* and *D*. In the entire course of the experiment there was not the slightest indication of light response, nor indeed was there more of a geotropic character. The final attitude was that indicated in *D*.

The other suspended specimen attached itself to the side of the overflow tube, and has continued head down, without appreciable change of aspect, the tube remaining almost perfectly straight from first to last. Both specimens seemed equally at ease, both equally active; but the one passed through the series of tubular contortions, the other remained absolutely indifferent. Incidentally it may be remarked that specimens are often found in nature attached to the under surface of bottom of boats or other substrata, much like barnacles or other sessile organisms; and hence it must be admitted that there is nothing especially unusual or unnatural in such an attitude. That the behavior of the one differed from that of the other is not more strange than that differences likewise appear between others.

Special Aquaria.—The second series of experiments were conducted in two special aquaria, mentioned above, and were prompted by two considerations First, the apparently negative character of the experiments began and carried forward in the large aquaria. It had seemed as if one should have more prompt and convincing results than appeared in the account just given. Secondly, it was desirable to have aquaria of a size and adjustment which made possible ready and effective control at all times, with such variation of tests as seemed desirable. Hence these smaller aquaria already described. They were set in a room whose light and temperature were under easy control, and were themselves of a size which enabled one to shift the position at any time it might seem desirable. It occurred to me that possibly the fact that in the first series the light had been diffuse rather than direct might have resulted in the somewhat negative behavior already noted. Again, it seemed desirable to be able to control both the direction and intensity of the light. Ac-

cordingly the special aquaria were made use of, and the following account is based entirely upon the behavior under the new conditions. Two were used for the definite purpose of making of one a control of the other. That is, given identical conditions of temperature, food, etc., will the mere difference of direction or intensity of light show itself in such measure as to warrant conclusions?

This series was begun on January 15 with twelve specimens, eight being placed in the experimental tank, and four in the control tank. The bottoms of the aquaria were covered by a layer of rather coarse, black sand to facilitate attachment, and at the same time to render any access of light from the bottom impossible. The test tank was covered on three sides and the top with an opaque hood, painted black on the inside and so adjusted as to render inspection easy without disturbing the specimens. In this tank the eight specimens were placed with heads facing away from the source of light. Similar disposition was made of the four specimens of the control tank. In about three days the specimens had apparently attached themselves, and on January 19, four days after beginning, one specimen began an upward curve. On the 21st several had shown such reaction and by the 25th several had curved upward to from 25 to 50 degrees. In the control tank similar responses began to appear.

On January 25, ten days after beginning, the record is as follows: Of the eight specimens two have curved toward the light, two are nearly vertical, two face toward the side, while two remain as planted. Essentially the same condition obtains in the control tank. One faces the window, one nearly vertical, and two as originally located.

At the end of four weeks, February 11, three show apparent light reaction, two are nearly vertical, two remain facing away from light, and one shows an indifferent curve laterally. The positions in the control tank remain as before. Repeating Loeb's experiment at this point, I now rotated the aquaria through 180 degrees, so that everything was changed directly about. Conditions went on as before, the test tank receiving light exclusively from one end, the control receiving diffuse light from the room as well as the direct light from the window. On February 25,

or fifteen days after the aquaria had been rotated, the conditions are as follows: Five specimens now face the light, while three face the opposite direction. But of the five now facing the light three were so placed in the readjustment made by the rotating, or reversing of the tank, so that only two have actually shown a possible light reaction. The three specimens which had been turned away from the window by this reversal had not shown the slightest response.

At this time the aquaria were again reversed, so that they came back to the original positions. It should be noted that in the control tank there had been no change induced by the reversal of the position, the specimens all remaining as before.

Another aspect of behavior may be stated in this connection. namely, an actual downward curve of several specimens. It was on first notice thought that possibly this might be due to the incurrent water, which happened to be in the region of one such case. However, it was later observed that other specimens quite remote showed the same thing, and on comparing similar conditions in the exhibition aquaria it was found to have its counterpart there. Hence it may be regarded as only another expression of the individuality of behavior which is more or less evident under all conditions.

The experiments with these special aquaria were continued to March 25, having thus been under operation for about ten weeks (January 13 to March 25), and have been in the present position for exactly one month. During this time there have been incidental shiftings on the part of various specimens, a bending this way or that from time to time, but only to be reversed later, or counterbalanced by opposite reactions of adjacent specimens. These have been noted from time to time during the course of all the experiments, and are not to be considered as orienting reactions, but rather expressions of the individuality of behavior characteristic, as I believe, of all grades of animal behavior. They correspond to what Jennings has designated as *trial reactions;* and in the present instances probably relate to food-seeking or respiration. These statements refer directly to conditions in the darkened aquarium; but they are quite as applicable to those of the control aquarium, and indeed, the

behavior of the specimens in this, while differing in various details, have shown a striking similarity to that of specimens in the former, as well as that of the first series in the large aquaria. As remarked in the outset, the entire series of experiments have involved no appreciable deterioration of the health or vigor of the specimens. As an evidence of this may be mentioned the fact that one very young specimen among those used in the control tank showed an apparently continuous growth, having nearly doubled its original size. The growth in this case seems to have been real and normal, and not *apparent* as was the case with *Hydroides*, mentioned in a previous section.

Third Series.—Early in March it was found desirable to change rooms in the laboratory, and I came into possession of one admirably adapted to light experiments. Advantage was taken of this circumstance to continue the experiments with *Spirographis* under light conditions which were exceptionally good. In the room were two large aquaria, one of which I devoted exclusively to this experiment. The aquarium was arranged with its side facing the window and at a distance of about two meters. By covering the back, ends and top of the aquarium with a black opaque screen, and with windows also provided with adjustable shades, one was able to directly control the light conditions at will, as to source, directness and intensity. The experiment was begun with eight specimens, all of which were placed with heads facing away from the light, and two others suspended head down by attaching them to sides of the overflow pipe, as in the similar experiment in series I. Other specimens were added a few days later making a total of twenty comprising the experiments. As before some two to four days were required for specimens to become attached to the aquarium. In the present case to insure prompt and precise location several were secured to a given place by putting over the terminal base of the tubes a small weight, such as a shell or rock fragment. As before the first indication of reaction was the usual upward curve of the oral end of the tubes, enabling the creature to freely expand the gills. This reaction has little, if any, relation to orientation movements, as it occurs usually in all cases and under almost all conditions, whether in light or darkness.

On March 25, ten days after the specimens were installed, only one had assumed a nearly vertical aspect. Others showed various phases of orientation, from ten to twenty, or thirty, or fifty degrees of elevation above the bottom.

On April 1, the following is the record. Four specimens with gills directed more or less toward the light; two with a vertical attitude; three oriented at right angles to direction of light, and facing darkest end of tank; nine remain oriented in original position, *i. e.*, facing away from light. The two suspended specimens behave almost exactly as in the previous case; that is, one perfectly unchanged and the other curved away from the pipe. Thus after nearly two weeks half of the entire lot remain abso-

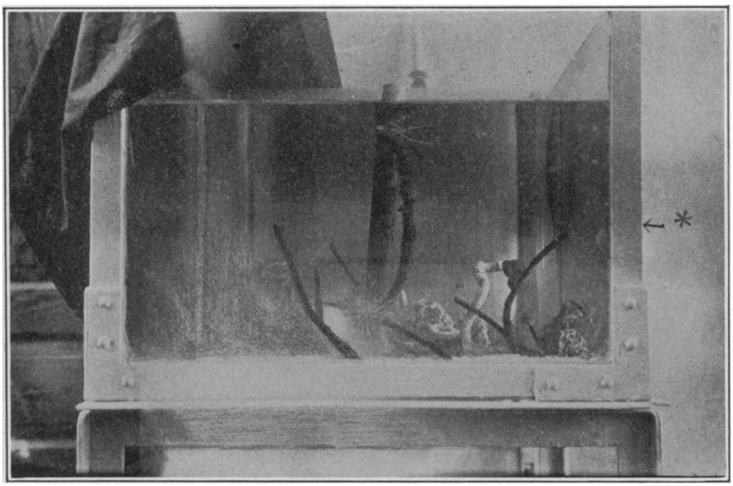


FIG. 4 is an end view of an experimental aquarium, the light coming from the right side at *. Of the eight specimens shown only one is facing the light, one is vertical, the others facing the dark side of tank.

lutely unchanged; of the others only five show any very clear reaction to possible light stimulus. The experiments continued under daily observation until April 12, a period of one month, with a final record as follows: Four specimens show a distinct curvature toward the light; nine show just as distinct inclination away from the light, in other words remain as originally fixed except the slight curvature upward; two are almost vertical; the other three occupy positions at right angles to the line of light.

The two suspended specimens continue as before, one absolutely as at first, the other with a definite crescentic curvature, but forty-five degrees away from light. Fig. 4 is from a photograph taken by Dr. S. R. Williams and gives a good impression of the orientation of such specimens as came within the view. It is taken from the end in order to show the relation of the tubes to light, which came directly from the right and into that side of the aquarium. Of the twenty specimens only eight are shown, and of these only one faces the light, one is almost vertical, the other six incline very definitely toward the dark side of the aquarium.

As will be seen, nothing especially new has developed beyond what has been found in connection with the earlier series. However, since here the conditions of light, temperature, etc., have been so ideal the results not only confirm those already given, but render them more certain and conclusive. It seems quite improbable that three series of experiments directed to a single end should have given uniformly erroneous results; moreover, it is equally improbable that any error of method should have vitiated all three series, varied as these are shown to be, and inspected as they were by several of my colleagues almost from the beginning. Nor is it possible that the matter of season could have been a modifying factor, for it coincided almost exactly with that of Loeb's experiments. That light has been shown to be a wholly negligible factor in relation to the behavior in question has not at any time been claimed. That it has been shown to have only a minor influence I believe the facts conspire to render very certain.

But we are not yet done with the problem. In his original account Loeb cited the behavior of *Spirographis* in the public aquarium as tending to confirm his experimental results "for the most part"! I have studied the problem in this aquarium with especial care during the entire course of my own experiments and have found the behavior to confirm *my* experiments, as the results will show. Let it be expressly understood that in these large exhibition aquaria the best efforts of many years have been directed to render them as nearly natural as it is possible to have such limited portions of the sea; and the fact that some

of their occupants have lived and thrived here for more than twenty-five years bears strong evidence to the measure of success in the effort to render them *natural.* In these aquaria *Spirographis* seems to find a fairly congenial environment, and thrives continuously in health for many months. For the sake of exhibition advantages the specimens have been planted, or disposed in such ways as afford the display of the gorgeous, flower-like gills to the best advantage. Hence some are located on the floor of the aquaria, others on the back and ends where rocky ledges afford suitable bases for their support. It ought also to be said that in order to render these aquaria the best possible exhibition cages the illumination is chiefly, and in some case wholly, from above; while the room itself is purposely kept dark, except for the light which diffuses outward from the aquaria. It becomes important that in reference to the problem before us this fact of the source and direction of light be borne in mind. On the assumption of the compelling potency of light it will be clear that in the case under examination there should be a fairly uniformly vertical aspect of the various specimens, whatever may have been their original position. The following are the facts: From several attempts it was determined with approximate accuracy that at this time there were about 150 specimens of *Spirographis* in the aquarium. These were disposed, as mentioned above, on the bottom, ends and back of the tank. Of the entire number about 90 were in more or less vertical attitude or with upward inclination, while 60 were otherwise inclined, that is, they were horizontal or inclining downward. The general facts are fairly well shown in Fig. 3, which is a photograph of the aquarium made by Dr. Sobotta, by whose kind permission I am able to use it in this connection. Of the 60 specimens of this adverse aspect slightly more than half were horizontally disposed, while the others, some 23 specimens, exhibited decidedly downward inclination. The picture will afford excellent illustration, though not taken at the time my observations were made.

Let us now attempt to analyze these facts and their bearings upon our problem. It may be stated at the outstart that gravity has little or no place in the behavior. Loeb has so concluded from his experiments, and my own go to confirm his verdict.

Both in experiments and in nature there seems to be no evidence of its operation. Specimens attach themselves to the bottoms of boats, to overhanging rocks, etc., and seem quite indifferent to its influence. We may therefore proceed to consider the main question at issue, namely, that of light.

Of the 90 specimens having a sub-vertical attitude about 60 were on the bottom of the aquarium, which leaves 30 of this class among those located on the back and end walls. In other words, twice as many of the vertical specimens were located on the bottom as on the sides. But let it be remembered that of the total 150 specimens in the aquarium about 94 were planted on the bottom while only 56 were located on the walls. Further, it is to be noted that those located on the bottom must assume a sufficient degree of elevation to afford a free expansion of the gills; to those on the walls this is not essential. On the other hand, of the 60 specimens which had assumed a horizontal, or downward attitude about 25 were among the bottom specimens, while the other 35 were among those attached to the walls. Expressed in percentages we have the following: Of the whole number about 60 per cent. showed a more or less vertical aspect, while 40 per cent. showed otherwise, *i. e.*, a downward inclination. Of those planted on the bottom about 70 per cent. showed a vertical tendency, and about 30 per cent. were inclined downward. Of those on the walls about 65 per cent. inclined downward, while 35 per cent. inclined toward the vertical.

Now, how shall one interpret these varying aspects? According to theory, "If the rays of light fall vertically from above into the aquarium, *Spirographis* directs its tube vertically upward, exactly as a stem grows vertically up into the air." In the case before us the *light comes vertically from above*, yet a large per cent. of the specimens fail to direct the tubes vertically upward. Of wall specimens 65 per cent. incline downward, or are horizontal in relation to light. Of those on the bottom the per cent. curving downward is much smaller, but still too great to be explained as merely incidental, or by the naive suggestion "Here, however, where free-swimming forms easily disturb the orientation of *Spirographis*, it is not so perfect as when all possible disturbing causes are avoided, as in an aquarium used only for such experi-

ment." Unfortunately for such explanation "free-swimming forms" are rarely present in this aquarium, the only specimens during my observations being the slow and delicate moving little sea horse, *Hippocampus*, whose presence among the relatively colossal *Spirographis* could hardly be of more influence as a disturbing factor than a few sparrows in an oak forest! In fact specimens of *Hippocampus* had been kept for weeks in one of the aquaria in which my special experiments were being made and would frequently attach themselves by their delicate prehensile tails to the tubes of *Spirographis* but without the least evidence of disturbance of any sort. One often finds the tubes of these annelids more or less loaded with tunicates, sponges, hydroids, etc., but there was never any appreciable sign of disturbance therefrom so far as their orientation was concerned.

I think it must be rather obvious that the behavior exhibited by these creatures under the sub-natural conditions of these magnificent aquaria conforms in all essentials with that found in the experimental tanks, and under both these tests there seems to be a fair equivalent of that to be observed in their native habitat.

Concluding Remarks.

The foregoing account, especially when taken as a part of the more extended observations already repeatedly cited ('06, '09), must make it more or less evident that so far from affording any support to the sweeping assumption of the identity of animal and plant heliotropism, based on the behavior of these organisms, strongly *suggests*, if indeed one might not say *warrants*, the very opposite. One might even go a step farther and say that it seems extremely doubtful whether the behavior of *Hydroides*, *Pomatoceras*, *Spirographis*, or any of the tubicolous annelids may be interpreted as an expression of tropisms at all. Without seeking in any way to discredit the possible rôle of light in relation to certain aspects of behavior, it may yet be fairly doubted whether it sustains any such determining influence as has been claimed by the exponents of the tropism hypothesis. Indeed the facts which have been passed in review show beyond reasonable doubt that in relation to these organisms it can have but a subordinate and incidental place. It seems perfectly certain that

there is not that degree of constancy, or character of reaction, in orientation which would warrant a tropic interpretation of any sort.

But on the other hand let it not be inferred that behavior is chaotic or beyond scientific explanation. As I have elsewhere pointed out, reactions and adjustments in relation to food-getting, respiration, etc., are among the most fundamental of all phases of behavior. These creatures must live, hence must have food; but they are sessile, and therefore must utilize such as may come within reach. Furthermore, they must respire, and hence must have room within which to expand the gills. All this implies that such colonial species must of necessity frequently resort to movements of readjustment directed to the above imperative ends. In most of these creatures it so happens that one and the same organ is involved in this dual function of food-taking and respiration; a fact of some significance in simplifying or complicating, according to condition, certain phases of behavior. To the writer it seems probable to the point of certainty that the aspects of behavior which have been under review are chiefly but varied expressions of these common functions. In other words, they are aspects of adjustment in the complex struggle for existence—varying modes in which each species has worked out its own special problem of life.

In the light of this mode of interpretation the complicated serpentine torsions of the tubes of *Hydroides* and *Pomatoceras* are the most natural expressions of just such "trial movements" as one might expect. Likewise the bending aspects of the flexible tubes of *Potamilla* and *Spirographis* are not mysterious enigmas over which students of behavior need array themselves in warring camps, but rather the simple expressions of those individual adjustments called for in the varying struggle of life, to the interpretation of which Huxley would have found necessary only "trained and organized common sense"!

I am quite aware that to speak of *individuality*, or *autonomy*, or *spontaneity* as factors involved in problems of animal behavior may to some exponents of mechanism seem "*no explanation*," and of significance only to the psychologist. But as I have earlier pointed out, *they are facts*, and they bulk large in the sum

total of animal economy and behavior. To recognize them *as facts* is not to imply thereby their *explanation;* but it *does* imply that they are no less entitled to recognition and explanation than any other classes of facts with which we have to deal. Facts are sometimes characterized as "stubborn things," they have ways of their own; they are tenacious of life; and sooner or later will compel respectful attention and explanation. As is well known, in his matchless account of the behavior of earthworms Darwin did not hesitate to employ a terminology which frankly assumed the presence in these creatures of nervous and psychic factors. While it may not be easy to prove that annelids have a high degree of intelligence, on the other hand he who essays to prove that intelligence has no part whatever in their behavior will hardly have an easier problem.

At no time has the writer questioned the important relations of physico-chemical factors to the phenomena of life and behavior. Further, he has not questioned the possibility of the correlation of these phenomena under *physical laws*, much as we recognize that phenomena of electricity and magnetism and gravitation are conserved under other natural laws. But this by no means implies that these latter species of energy have not their own *special laws*, some of which are already known while others have thus far defied definition and correlation. So, in the matter under review, what he *has* questioned is the very different postilate, that *known properties* of chemistry of physics in any of their *known interactions* afford adequate definition and explanation of *all the facts;* or that *known physical laws*, as applied by the sponsors of mechanism, are convincingly sufficient. It is against the arrogant assumption that a fact of behavior, or an expression of emotion or affection, is never explained till cast into some physical or mathematical formula, that protest has been iterated. In directing attention to the possible interaction of well-known psychic factors in behavior there is merely the plea that similar recognition be given to them as to the former and, as suggested above, they be included in the category of behavior calling for explanation. However independent or unrelated may appear certain of their expressions it is not assumed that in any scientific sense they are mutually

exclusive, nor that the one class of phenomena are any less related to causal antecedents than the other. But it *is* maintained that while in some cases these antecedents may be known, and lend themselves to direction and control, on others they are as yet absolutely unknown and more or less beyond prediction or control. And furthermore, it is believed upon experimental evidence that certain aspects of behavior may be more or less variable under any given set of antecedents or conditions; in other words, *given stimuli do not always evoke the same response;* in fact, *much* of *behavior* is *indeterminate* in terms of *existing knowledge.* But so far from implying a reactionary attitude toward the value and importance of continued experimentation, the writer would hold the very opposite. It is well that one pause now and then and take stock in science as well as in business. That problems of behavior are complex beyond earlier anticipation goes without saying. The same must be admitted of every problem of biology. Only the biological pessimist will find occasion to contemplate intellectual suicide because he finds the dogmas of his science in process of revision!

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